



Digitized by the Internet Archive  
in 2012 with funding from  
LYRASIS members and Sloan Foundation

<http://archive.org/details/threedecadesofch00coll>

Bulletin 653

November, 1962

# **Three Decades of Change in an Unmanaged Connecticut Woodland**

**STEPHEN COLLINS**



THE CONNECTICUT AGRICULTURAL EXPERIMENT STATION  
NEW HAVEN

## CONTENTS

Introduction .....	1
Successional History From Permanent Plots .....	2
Soil, Climate, and Land Use .....	3
Methods .....	5
Composition and Structure .....	8
Site and Height .....	14
Growth, Reproduction, Defect, and Death .....	15
Discussion .....	23
Conclusions .....	28
Summary of Observations .....	30
Names of Plants in This Bulletin .....	31
Literature Cited .....	32

### Acknowledgments

The author is grateful to Henry W. Hicock, Forester Emeritus of this Station, for establishing the Plots and caring for them through the years; to Alexis R. Olson for sharing the work of the census of 1957; and to Paul E. Waggoner for helping prepare this Bulletin.

# **Three Decades of Change in an Unmanaged Connecticut Woodland**

STEPHEN COLLINS\*

This study deals with the trees and shrubs in an unmanaged forest—their distribution, change, and causes of change. These changes have been recorded for 30 years on the 50-acre Cox Plot in the Meshomasic State Forest in Portland, Connecticut.

Compared with the value added to materials by manufacturing in Connecticut, the annual timber cut is of little economic consequence. But the extent of the forest—it covers two-thirds of the State—suggests values that far transcend those of forest products alone. Urban, suburban, and industrial Connecticut could not function without the water stored and gradually released by the woodland. Recreation in the forest—hunting, fishing, hiking, and touring—are also part of Connecticut life.

Whether your view of the woodland is colored by economic, recreational, or aesthetic considerations, one fact remains: the forest is here and it has doubled in area in the last century. Very likely it will continue to increase in area, and certainly it will increase in value. One cannot understand our woodlands, nor manage them intelligently, without first knowing the natural result of no management. The unmanaged woodland thus becomes a necessary benchmark with which varying degrees of management may be compared.

Cox Plot mirrors the lack of management typical of much Connecticut woodland. It is now beginning to reveal what happens when natural forces alone operate in a woodland. The image will become even clearer with time. But the Plot may already show whether a forest of low quality will automatically improve. If such improvement has occurred, how much time was required? If not, should the concept of automatic improvement by natural forces be abandoned?

Without knowledge of changes that have occurred, forest management is on a trial-and-error basis. Such management may be costly even with annual crops, where mistakes may be corrected in a year or two. It may be disastrous in the woodland, where mistakes may not be apparent for decades and corrections may require still more decades. Prudent management of woodlands, therefore, begins with realization that natural trends are operating, that they will continue to operate, and that it may prove both efficient and effective to work with, rather than against, Nature.

---

\* Formerly on the Station staff. Present address: Southern Connecticut State College, New Haven.

## SUCCESSIONAL HISTORY FROM PERMANENT PLOTS

In an old field, various species of plants succeed each other as time passes. In a forest, individuals grow or die while the same species persist. Consequently, methods of studying succession in the old field may be inappropriate in the forest.

In the old field, succession can be inferred in minimum time by the method of alternating areas. Several areas in different stages of regrowth are selected in close proximity on essentially similar sites. From such a floristic spectrum, one infers a presumed time sequence. Lutz (1928), Raup (1940), and Bard (1952) provide classic examples of this technique.

Following the development of a continuous canopy, however, succession is not marked by great change in composition; and hence the assignment of age to plots is not reliable. Changes in growth and number are more important than changes in composition. Thus, in the forest there is no substitute for the patient re-examination of permanent plots.

The permanent Cox Plot was chosen in 1927 and described in Bulletin 330 of this Station (Hicock *et al.*, 1931). Without the detailed early records in the Station files, and without the cooperation of the State Park and Forest Commission in keeping the Plot essentially free from human disturbance, the findings now reported could not have been made.

When the Plot was chosen, the vegetation had passed through the old field stage, and there was a continuous canopy. Along sample strips, every woody stem was identified, measured for diameter, and mapped as to location. The permanent location of these stems enabled remeasurements on the same stems so that sampling error was considerably reduced. This

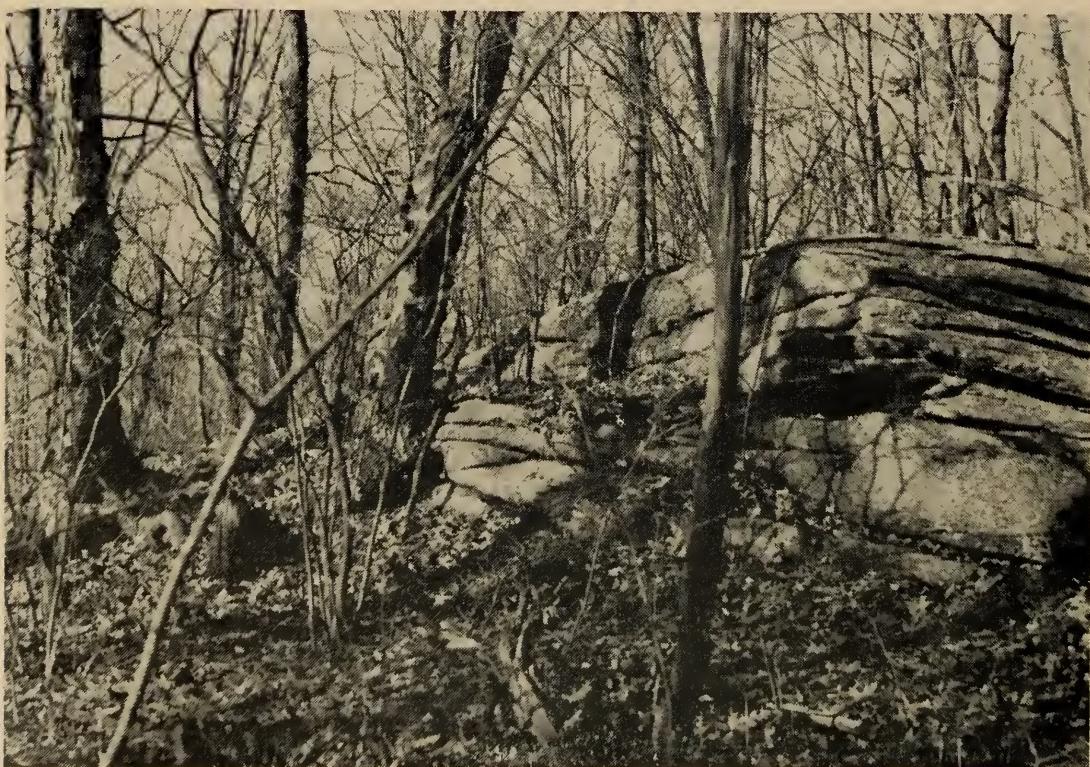


Fig. 1—An outcropping of Glastonbury gneiss on the Plot but outside sample strips.

reduction in variability was needed in order to study succession in the later stages found in the forest, because there is little change in composition, and growth must be the index of change. And so, in the woodland, changes over a period of time are quantitative, while those in the old field are qualitative and are emphasized by changing composition.

We now examine the Cox Plot against its background of soil, climate, and land use.

### SOIL, CLIMATE, AND LAND USE

Cox Plot is located in Meshomasic State Forest, Portland, Middlesex County, Connecticut. It is near the western end of the Eastern Highlands, a region of metamorphic rocks and glaciated soils. The underlying rocks are Glastonbury gneiss, but exposures of outcrop are uncommon (Fig. 1).

Topography is rolling with a few outcrops in the northwest corner of the Plot. The steepest slopes are 35 and 32 per cent; all others are gentle. Bouldery areas are frequently found on the lower slopes, commonly in wet areas. Differences in elevation do not exceed 120 feet and the absolute elevation above sea level is about 400 feet.

As classified in 1927 (Hicock *et al.*, 1931), soils are: Hinsdale fine sandy loam stony, Hinsdale loam stony, Whitman loam stony, muck, and rough stony land. A small intermittent stream drains a swamp northeast of the center of the Plot.

Average annual precipitation is 46 inches. The average dates of the first and last killing frost are April 25 and October 15. High winds from the east and northeast associated with tropical storms do not strike the Plot



Fig. 2—New York fern persisting on a former charcoal hearth.

with full force because a ridge 800 feet above sea level lies to the east of the Plot and intercepts the winds.

Land use in Connecticut has been dominated by three great events: clearing for agriculture, cutting for charcoal (Fig. 2), and the blighting of the chestnut (Fig. 3). All of these must surely have affected the Cox Plot, which is typical of much of Connecticut woodland.

Red cedar<sup>1</sup>, common juniper, gray birch, and hazelnut cannot become established in shaded woodlands but may linger in an area which grows back to forest. They thrive only in the open and their presence on



Fig. 3—Remains of a large American chestnut that have persisted for about a half century.

the Plot indicates an earlier, more open period, when the area may have been in pasture. Another indicator of pasturing, barbed wire scars, persists on trees in the Plot. The ground is not so rocky that pasturing would be impossible. No evidence of stone walls was found on the Plot. This suggests that the land probably was never tilled. Fences were of chestnut rails.

Original notes from the first survey (Hicock *et al.*, 1931) show that most of the trees were about 30 years of age in 1927. Older wolf trees were also present, interfering with the growth of smaller trees, but the bulk of

<sup>1</sup> See page 31 for list of common and scientific names.

the trees on which early increment borings were made went back three decades. This dates the land abandonment before the late 1890's.

Since establishment of the Plot in 1927, records of events are complete. Slash was burned on less than 1 per cent of the 6.5 per cent sample area. A dirt road was built, occupying about 3 per cent of the sample area. Across most of the sample strips and in about 5 per cent of the sample area, a bed for a proposed road was cleared of trees and boulders. Some chestnut that was dead in 1927 was later cut and stacked. The important fact is that the human disturbances of greatest consequence on the Plot antedated 1927. These many factors produced the vegetation of the Plot, which we now describe.

## METHODS

*Sampling.* The Cox Plot is a 14- x 36-chain rectangle with the short dimension running on a magnetic north-south axis. Ten 14-chain north-south lines are equally spaced at 4-chain intervals and cut across contours. (A chain equals 66 feet.) At 2-chain intervals along these base lines stakes were set and surrounded by stones.

Stem measurements were taken on strips 16.5 feet wide and centered on these north-south base lines. This arrangement provides 14 sample strips, 16.5 feet wide and 14 chains long, giving a total of 3.45 acres in the sample of the 50 acres in the Plot (a 6.5 per cent sample).

In 1927 and 1937 all trees, witch hazel, alder, and poison sumac whose stems were 0.6 in. d.b.h. (inches diameter breast high) and larger were mapped and measured. Because the trees 10 in. d.b.h. and larger were not numerous in the original strips, they were measured over strips twice as wide. To be counted and measured, the center of a stem or clump had to fall within the sample strip.

In 1957 all plants whose stems were 0.5 in. d.b.h. or greater were measured.

*Diameter and height.* In 1927 and 1937 the d.b.h. was measured to the nearest inch, and in 1957 to the nearest 0.1 inch. The difference between the squared diameters of each stem was the indication of growth.

In 1957 the height of all dominant trees was estimated with an Abney level.

*Cover and crown.* "Cover" expresses the area of foliage at all levels. To visualize this type of measurement, imagine the sun directly overhead so that each tree casts a shadow. If we stretch a tape along a baseline, we can then read the length of tape shaded by each crown (Buell and Cantlon, 1953). If we add the segments shaded by each species, we have a quantitative indication of its leaf area or photosynthetic mechanism. When summed by crown class, cover describes structure of the wood.

Fig. 4 illustrates the nature of cover measurements, indicating areas overhung by no foliage as "space." In some cases two or more trees will have overlapping crowns. The segments under each were recorded so that areas of overlap made the total cover along the baseline greater than the length of the baseline. Where many crowns overlapped the shade was deep, while nearby no foliage might cover other sections of the baseline.

In practice, in 1958, we sighted on crown edges with a 6-foot rod which hung from a pivot. This made the rod self-plumbing. It swung in the

same plane as the baseline. The rod man straddled the line, moving to a point directly under a crown edge. By sighting along the rod he corrected his position until he was directly under the crown edge. Here he read the tape and moved to the other edge of the crown for his second reading.

The diameter of each tree shading the line was previously measured, and its crown was classified according to its position in relation to other trees. Thus each dominant tree was class I; each codominant tree class II, intermediate trees fell in class III, and suppressed trees in class IV (Hawley and Smith, 1954).

Some trees with bases outside the sample strip leaned into the strip, and their crowns fell over the baseline. Such trees were included with the cover measurements, and their crowns were classified. However, we did not measure their diameters. In addition, the number of trees leaning from the left, and the number leaning from the right side of the sample strip and covering the baseline, were counted; this revealed the direction of the tilt.

*Seed and reproduction.* In 1958, 1959, and 1960 we observed the production of seed on dominant trees on the sample strips to learn year-to-year variation and to learn how much sound seed was produced.

Sprouted acorns of red oak were planted in both scarified and litter-covered spots to learn the fate of seed that fell upon the forest floor and

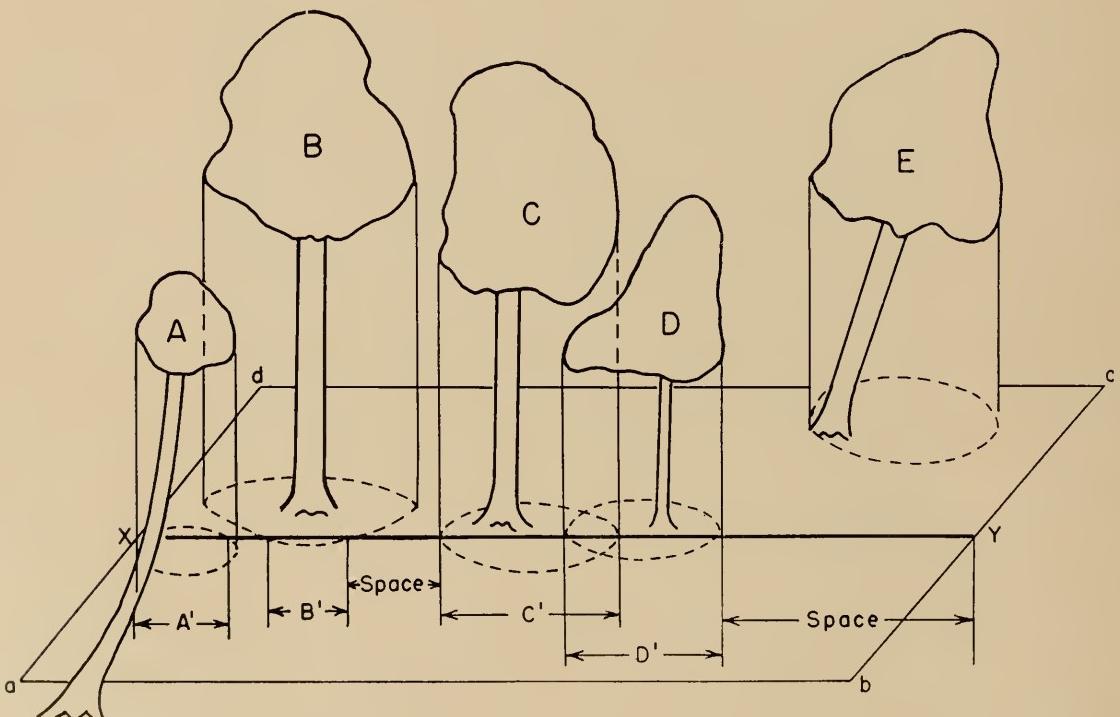


Fig. 4—Cover measurement. Tree diameters were measured over area *abcd* where *bc* is 16.5 ft. Cover was measured along *xy*. *A'*, *B'*, *C'* and *D'* are the segments of *xy* directly beneath crowns *A*, *B*, *C*, and *D*. Cover = *A'* + *B'* + *C'* + *D'* and may be greater than *xy* where overlapping crowns, as *C* and *D*, are numerous. Space equals any segment of *xy* not beneath foliage. Although the base of tree *A* is outside *abcd*, its trunk is tilted, its crown covers a segment of *xy*, and its species, its crown, and *A'* are recorded. On the other hand, although the base of tree *E* is inside *abcd*, its crown does not cover *xy* and it is omitted from cover measurement.

survived the winter. We well knew that most acorns would be destroyed over winter and were concerned only with the few seeds that might survive.

*Tree defects and mortality.* In 1957 defects were recorded for every dominant tree and in many cases for others. Defects were classified as stem defects and crown defects.

A stem was considered defective when it was tilted, bowed, or crooked. A crown was classed as defective because of breakage, top death, or vines. Scars were classified according to openness, size, height, and cause. No attempt was made to find internal defects.

Resurveys in 1937 and 1957 indicated the net mortality between measurement periods but not between years. Over such extended periods, evidence of the cause of death of a stem is apt to be lost through decay. Accordingly, the mortality of stems was recorded for the 3 years 1958-60 to learn the nature of mortality. All stems 0.5 in. d.b.h. and larger, and alive in 1957 were examined annually.

*Soil moisture.* The soil moisture regime was classified in the sampling strips as follows:

1. Muck.
2. Very wet: water table at surface over gray, oxidized, usually sticky soil.
3. Wet: mottling near surface, less than 4 in. organic matter accumulated, usually a shallow brown oxidized layer present.
4. Moist: water or mottling near surface, aerated 12-16 in.
5. Medium: with temporary moisture reserve on lower slopes, but no visible mottling or standing water table.
6. Dry: upper slopes.
7. Very dry: shallow ridge tops, or deep coarse sands.



Fig. 5—The dense shrub understory in a red maple swamp. One of the sample strips ends in this swamp.

## COMPOSITION AND STRUCTURE

*Communities.* Homogeneity of vegetation was an important criterion in choosing the Plot. Even today there has been no differentiation, and one sees no difference in physiognomy caused by variation in layering, life form, or other features. An exception to the homogenous oak upland is the swamp with its marked shrub layer (Fig. 5).

Because the vegetation on the swamp was not previously charted, the recent survey provides no basis for assessing changes that might have taken place on it. Furthermore, the area occupied by the swamp was minor in comparison to the rest of the Plot.

The variation in rockiness might seem to be useful in delimiting a separate community, but no distinctive vegetation was noted in relation to rockiness. Since the underlying bedrock outcropped infrequently (Fig. 1), and the rockiness was limited to detached materials on the surface of the Plot, a thin soil which might be expected to create an extreme habitat was absent. The outcrops occurred between the sampling belts, and so no record of change on them is revealed by data. However, certain species could persist on such areas (butternut was one), and others (such as the ebony spleenwort fern) were limited to such outcrops. The minor extent of this community and the swamp community make them of only passing interest. Furthermore, since these communities have developed on extreme substrates, no great changes in their areal extent are anticipated which would in any way encroach upon the major community of the Plot—a hardwood community dominated by oak.

Although neither rock nor swamp communities could displace the major hardwood community because they are under strict edaphic control, another community immediately adjacent to the Plot potentially could be-



Fig. 6—A small hemlock that was severely browsed.

come important in replacing the hardwoods. This is the hemlock community.

Hemlock trees outside of the Plot were sufficiently clustered to justify designation as a community. They were most numerous on a poorly drained area, but also appeared on occasional mounds of soil that had fallen in heaps from the root systems of windfallen trees. Since scattered hemlocks, some of them with saplings about them, were found on the Plot itself, invasion by a hemlock community is possible.

However, this has not happened in 30 years. We attribute this to the browsing of deer and, perhaps, rabbits which pruned small hemlocks severely (Fig. 6). The growth of hemlock was undoubtedly retarded also by the shade of hardwoods, and seedling establishment was retarded by the continuous, thick litter of oak leaves. No fires have occurred on the Plot since 1927; a fire today could destroy all hemlock reproduction.

Hemlock replacement could be speeded if openings were created and seed beds were formed by uprooted trees. However, we have noted that the Plot is sheltered by surrounding hills. The hurricane of 1938 did not uproot any trees.



Fig. 7—A red cedar that has died but is held up by an oak.

We point out these possibilities for hemlock to emphasize the uncertainty in predicting succession in an environment not manipulated by man. However, an understanding of possibilities should enable us to establish hemlock readily if this is desired.

*Structure.* As the photograph on the cover of this Bulletin shows, the Plot is a typical cutover deciduous woodland with numerous multiple-stem trees or sprout groups. The canopy is nearly continuous except on the swamp. The shrub thickets are not so dense that they impede walking. Occasional white pines or hemlocks on the Plot are the only conifers, except for the stems of persisting dead red cedars (Fig. 7). Before blight, chestnut may well have been the dominant species, but today the oaks predominate.

A mere recital of species would mean little to a person unfamiliar with those in the area. A structural description based upon form of stem and leaves, on strata, and cover, is more widely understood.

On the higher land a continuous canopy of deciduous trees (mostly *Quercus* spp.) with broad, simple leaves covers most of the Plot. In this upland forest there are only a few species with compound leaves (*Fraxinus americana* and four species of *Carya*). Conifers are present and may appear significant on a floristic basis because approximately 10 per cent of all species are conifers. When, however, one examines the contribution of the conifers to the number, volume, and cover, it is unimportant (Table 1). Only one of the conifers, *Tsuga canadensis*, might increase in importance, because the remaining ones, *Juniperus virginiana* and *Pinus Strobus*, cannot long survive when shaded.

Underneath the continuous canopy are suppressed trees together with five species of deciduous, simple-leaved, small tree species which lack the inherent capacity to grow into the canopy (*Cornus florida*, *Ostrya virginiana*, *Carpinus caroliniana*, *Betula populifolia*, and *Amelanchier arborea*). Nowhere do any of these suppressed or small trees mass to produce a definite layer.

Table 1. The percentages of tree species, individuals, and basal area within the Cox Plot, 1957

Species*	Number of individuals size class (d.b.h.†)				Basal area†
	1-3 in.	4-6	7-9	≥ 10	
<b>Deciduous</b>					
Simple leaves .....	68	89.9	93.7	87.8	98.8
Compound leaves .....	21	10.1	15.8	12.1	1.2
Needle .....	11	....	0.5	....	.001
Sample number or area on 3.45 acres .....	594	385	190	172	306 ft. <sup>2</sup>

\* 28 species found within the Plot.

† Diameter breast high at 4.5 feet.

Among shrubs, deciduous, simple-leaved, rarely lobed, or compound-leaved species predominate with only two evergreen species present. One of these evergreens is broad-leaved (*Kalmia latifolia*) and the other is a lingering pioneer species with needle-leaves (*Juniperus communis*). No longer do the shrubs produce impenetrable thickets, although the thin colonies of some (*Kalmia latifolia* and *Corylus* spp.) suggest that they once did. Lianas (*Vitis* sp. and *Smilax* sp.) are rare. At the herb level, deciduous perennials predominate, but evergreen ferns (*Polystichum acrostichoides*) and club mosses (*Lycopodium* spp.) form large colonies which are conspicuous after autumn leaves fall.

A litter of deciduous leaves forms an almost unbroken cover except over boulders, stumps, fallen logs, and mounds of soil from uprooted trees and mammal burrows. Mosses and lichens grow where litter is absent.

The only swamps within the Plot have broken, exclusively deciduous canopies (*Acer rubrum* and *Fraxinus americana*). Under the openings in the canopy, a variety of shrubs grow thick in contrast to their sparsity under the closed canopy of the upland forest.

Both shrubs and trees are confined to islands created by the overturning of trees and the accumulation of moss. Whether the shrubs consist of many separate stems joined underground (*Clethra alnifolia*) or form spreading clumps (*Benzoin aestivale*), they lean over gaps between mounds.

Beneath the shrubs and upon the same islands, deciduous herbs (*Maianthemum canadense*) grow. Mosses are abundant. They form continuous mats and dominate the islands. Although some litter accumulates on the mounds, it blows off their steepened sides and breaks down quickly.

In summary, the deciduous and continuous canopy, except in the swamps, is the dominant feature of Cox Plot.

*Cover and dominance.* The cover on the Plot is tabulated by species and crown class in Table 2. The species are grouped arbitrarily into: major, contributing more than 5 per cent of basal area at some time; minor,

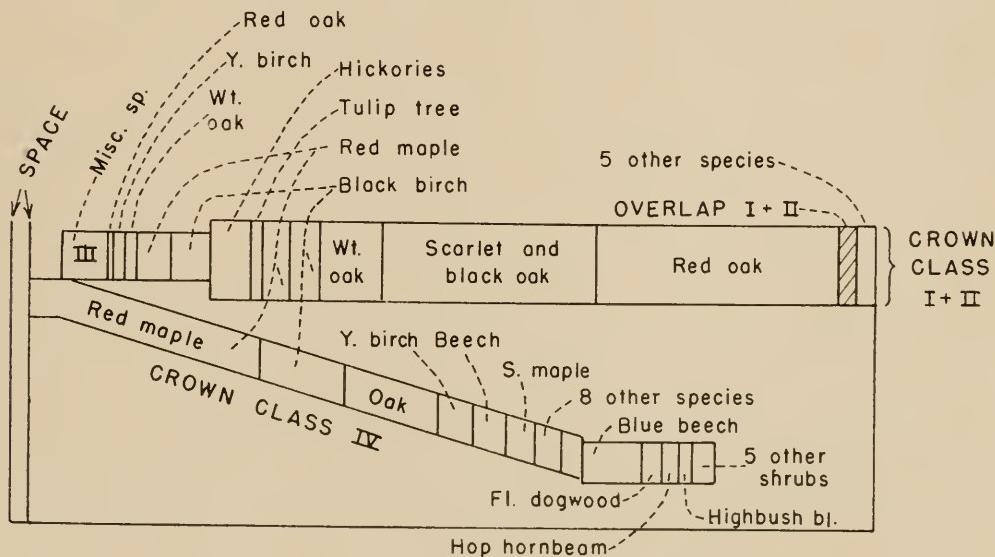


Fig. 8—Structure. The width of the rectangles indicates the amount of cover, and their vertical position indicates the position of their crowns in the forest.

Table 2. Tree cover in 1958

	Cover in all crown classes		Percentage in each crown class		
	Feet	%	Dominant, codominant	Inter- mediate	Suppressed
<b>Major species</b>					
red oak . . . . .	3,931	23	89	3	8
red maple . . . . .	3,346	19	10	13	76
scarlet oak . . . . .	1,660	9	90	7	3
black oak . . . . .	1,398	9	84	3	14
white oak . . . . .	1,238	8	52	12	36
black birch . . . . .	1,700	11	19	23	57
white ash . . . . .	307	2	26	10	64
bigtooth aspen . . . . .	30	0	78	22	0
<b>Minor species</b>					
sugar maple . . . . .	419	3	8	21	71
yellow birch . . . . .	640	4	17	22	61
tulip tree . . . . .	203	1	76	6	18
black cherry . . . . .	10	< 1	...	100	...
shagbark hickory . . . . .	111	1	34	37	29
pignut hickory . . . . .	324	2	42	10	48
<b>Unimportant species</b>					
chestnut oak . . . . .	9	< 1	...	100	...
beech . . . . .	461	3	...	14	86
American elm . . . . .	17	< 1	...	...	100
mockernut hickory . . . . .	123	< 1	79	...	21
bitternut hickory . . . . .	19	< 1	45	...	55
American chestnut . . . . .	229	2	...	...	100
hemlock . . . . .	20	< 1	...	...	100
sassafras . . . . .	31	< 1	...	...	100
basswood . . . . .	44	< 1	52	43	4
tupelo . . . . .	87	1	...	...	100
gray birch . . . . .	14	< 1	...	...	100
paper birch . . . . .	11	< 1	...	...	100
Total space . . . . .	14,761	100	...	...	...
Open space . . . . .	1,571	...	...	...	...

contributing more than 1 but less than 5 per cent; and unimportant, never contributing more than 1 per cent. The openings comprise only 5 per cent of the area. The structure is derived from these data and presented graphically in Fig. 8.

The canopy is largely dominant and codominant oaks, mainly red, scarlet, and black. Trees of intermediate size contribute much less to the canopy, with both black birch and red maple being the greatest contributors. The overlap of dominant and codominant trees is small, and hence the canopy admits considerable light.

Among the suppressed trees that grow below the canopy of crown classes I, II, and III are the transgressive members: trees growing into or capable of growing into the canopy. Red maple is the single most important

species and contributes twice the cover of black birch (Fig. 8). The total transgressive oak cover is about equal to the cover of black birch. The remainder of the transgressives includes yellow birch, beech, and sugar maple. Here, too, are found the sprouts of American chestnut, which never fruit or grow tall as they do on open roadsides before they are blighted.

Making up the shrub layer are species incapable of growing into the canopy (Table 3). Some reach the size of small trees, but never form anything resembling an intermediate layer, since their cover is only one-seventh of the ground area. Among these are blue beech, flowering dogwood, hop hornbeam, highbush blueberry, and others playing minor roles.

Table 3. Shrub and small tree cover in 1958

<i>Species</i>	<i>Length of cover, ft.</i>
flowering dogwood .....	227
blue beech .....	647
hop hornbeam .....	207
shadbush .....	21
witch hazel .....	108
poison sumac .....	14
spicebush .....	20
highbush blueberry .....	132
azalea .....	350
Total .....	1,419
Open space .....	7,689

The great contribution to the canopy of a single group of trees, oak, and the lack of windfalls make a canopy capable of suppressing growth beneath. In contrast, on a ridge swept by storms, the canopy is fractured and the crowns overlap (Collins, 1957). In the Cox Plot, however, none of the suppressed but tolerant beech, sugar maple, or hemlock give evidence of growing into the canopy and hence becoming influential members of the community. Although windfalls were generally lacking, there was evidence that wind had tilted the trees from east to west. Of 1,488 stems leaning over the baseline, 846 had their bases on the east side of the sample strips. In 10 of the 10 sample strips, more stems tilted from the east than from the west, an observation that would be encountered only 1 in 1,024 times by chance alone.

Cover or areal spread of foliage as shown here probably is a better measure of light utilization by a tree than is basal area of stem. The struggle for light being critical, cover measures the ecological importance of a species, while basal area or volume of stem measures the economic. The measurement of cover also reveals the structure of the forest. The structural arrangement of forest layers in turn will determine the patterns of succession. The height of trees is, however, the accepted indicator of site quality.

## SITE AND HEIGHT

*Moisture.* Whereas basal area, increment, or numbers of trees depends upon the number of trees originally present on an area, tree height is influenced less by such sources of variability. The height of the dominant oak was about 70 feet in 1957 when the trees were 55 to 70 years old. This indicates that the site is a rather good one, for McIntyre (1933) found the mean height on the best of six site classes was 78 feet at 70 years in Central Hardwood oak forests in Pennsylvania.

Probably the most significant thing that tree height reflects is soil water content. No elaborate methods are needed to verify that trees grow taller and straighter at the base of slopes than on the upper slopes and hilltops. In winter it is noted that distant trees follow this pattern from lower slopes to ridge. Lower slopes are excellent growing sites, but too moist conditions in swamps lack good aeration. Furthermore, near swamps the soils become saturated following heavy precipitation, and this disposes trees to topple in the wind. The larger the tree, the more likely it is to topple. Thus on swamps and their borders, trees are shorter just as they are on dry hilltops.

That the trees of Cox Plot follow this rule is seen in Table 4; the trees on the soils of intermediate moisture are taller than the trees on the dry soil or the few trees found in the muck and very wet soil.

*Stoniness.* While moisture is important to trees, another important factor in the soil is stone. Stones displace soil that would have stored water and released nutrients; they also change infiltration and leaching of water, and change the temperature course in the soil. Studies made elsewhere have shown that stoniness retarded height growth of oak on upper slopes but had no effect on the deep soil of lower slopes (Trimble and Weitzman, 1956).

The round, detached stones of the Plot retarded growth of trees on the moist soil, but increased it on the soils classified as medium in moisture. These effects were significant in trees 25 to 30 years old (Table 5). The trees 35 to 40 years old behaved in the same manner. Thus, on moist sites

Table 4. Height on six soil moisture classes, 1958

Class	Age 55-60		Age 65-70	
	Number of trees	Mean height, ft.	Number of trees	Mean height, ft.
Muck . . . . .	1	48.0	....	....
Very wet . . . . .	1	59.0	....	....
Wet . . . . .	30	70.2	9	73.1
Moist . . . . .	73	72.8	37	73.5
Medium . . . . .	49	69.9	68	75.3
Dry . . . . .	28	67.4	28	68.0

Standard deviation of height, 5.5 feet.

we have observed the usual disadvantage of stones, and at the same time observed a surprising and unexplained advantage of stones on the soil classified medium in moisture. This effect of stones and that of moisture concludes the list of soil factors whose effect upon site quality can be detected on the vegetation standing upon the Plot in 1957. Now, growth will be employed as an indicator of changes.

Table 5. Stoniness and height of 55- to 60-year-old trees

Class	Moisture class			
	Moist		Medium	
	Number	Height, ft.	Number	Height, ft.
Very stony .....	20	69.3	0	....
Stony .....	37	73.4	33	71.2
Not stony .....	14	76.6	14	67.2

### GROWTH, REPRODUCTION, DEFECT, AND DEATH

*Growth of basal area.* Between 1927 and 1957 the total basal area of the stems on the Plot increased from 75 to 117 square feet per acre, an increase of 56 per cent (Table 6).

The basal area of most species increased from 1927 to 1957 (Table 6). Outstanding among the major species were red, scarlet, and black oak, and outstanding among the minor was tuliptree; these more than doubled their area. Although unimportant in amount, chestnut oak, beech, and hemlock also more than doubled in basal area.

The gain or loss in importance of a species in the stand can be gauged by whether it provided a greater proportion of the basal area in 1957 than it did in 1927. Those that remained the same or became more important were four major species—red, scarlet, and black oak, and black birch; the three minor species—sugar maple, tuliptree, and shagbark hickory; and four unimportant species—chestnut oak, beech, mockernut hickory, and basswood (Table 6).

The change in diversity of the stand can be shown in the change in the proportion of the basal area contributed by oak. In 1927 it contributed 49 per cent; in 1957, 63 per cent. In addition, the number of species contributing 5 per cent or more of the basal area of the stand fell from eight in 1927 to six in 1957. Thus, in this unmanaged stand, oak became more predominant as the years passed. In spite of this basal area increase of oak, it has failed to reproduce from seed.

*Reproduction.* The basal area of a species is a useful measure of its present status. However, it is greatly influenced by large stems, while minimizing the contribution from small ones which may control the future forest. Only those species with recruits ready to fill the ranks left vacant by larger members will be of future importance.

## CONNECTICUT EXPERIMENT STATION

Table 6. Growth, reproduction, and death on the Plot

Major species	Percentage of basal area represented by the various species		Modal diameter 1957	Persisting individuals 1927-57	New stems		Sprouts as % of new stems	No. of trees that died 1927-37		
	in 1927				1927-37					
	(1)	(2)	(3)	(4)	(5)	(6)				
<i>Increasing proportional basal area</i>										
red oak	17	27	6,11	159	3	4	50	193		
scarlet oak	8	12	6	58	0	0	0	34		
black oak	7	12	11	67	0	3	0	90		
black birch	..	8	1	124	9	115	10	203		
<i>Decreasing</i>										
red maple	15	13	2	422	11	140	61	798		
white oak	17	12	7	120	0	0	0	600		
white ash	5	3	2,4	66	0	27	70	295		
bigtooth aspen	..	8	T	6	4	0	1	120		
<i>Minor species</i>										
<i>Increasing proportional basal area</i>										
sugar maple	1	1	1	50	2	18	33	61		
tuliptree	2	3	11	16	0	3	100	12		
shagbark hickory	..	2	5	36	0	2	50	35		
<i>Decreasing</i>										
yellow birch	..	3	1	66	2	30	53	121		
black cherry	..	2	T	4	0	0	0	104		
pignut hickory	..	2	1	2	29	0	5	166		

T Trace.

Table 6. (continued)

	Percentage of basal area represented by the various species		Modal diameter 1957	Persisting individuals 1927-57	New stems		Sprouts as % of new stems	No. of trees that died 1927-37				
	in 1927	in 1957			1927-37	1937-57						
<i>Unimportant species</i>												
Increasing proportional basal area												
chestnut oak	T	12	1	0	4	0	2					
beech	T	1	22	3	43	30	18					
mockernut hickory	T	1	5	0	1	0	49					
basswood	T	1	7	0	0	0	8					
Decreasing												
American elm	T	0	3	1	0	0	20					
bitternut hickory	T	6	3	0	0	0	20					
American chestnut	T	1	2	0	100	100*	23					
red cedar	T	0	0	0	0	0	4					
hemlock	T	4	2	0	0	0	0					
sassafras	T	1	6	0	26	12	26					
tupelo	T	1	21	1	3	33	36					
butternut	T	0	0	0	0	0	15					
Total basal area ft. <sup>2</sup> /A	75	117	....	....	....	....	....					
Total individuals in sample strips	....	....	1295	32	525	....	3053					

T Trace.

\* Although only 10 had companions, no seed has been produced in many years and all 100 were certainly sprouts.

The rates and kind of reproduction also reflect present and past processes in the forest.

The number of new trees appearing in our tables is actually the number of small stems which grew to 0.5 inches d.b.h. after 1927. There was no way of knowing how many of the recruits, or "ingrowth," started from seed after 1927 and how many already existed in 1927 as stems too small to measure. It was, however, possible to identify half of them as sprouts, while the others were either seedlings or were sprouts lacking a measurable companion.

To learn something of the reproduction of each species we compared the number of stems arising between 1927 and 1937 (Table 6, column 5) with the number present throughout the study (column 4). During these 10 years, reproduction was too low to permit meaningful analysis; only 32 stems appeared. Fortunately, 525 stems appeared in the 20 years after 1937 (column 6) and these permit analysis. In other words, stems appeared eight times as rapidly between 1937 and 1957 as in the earlier decade (Fig. 9).

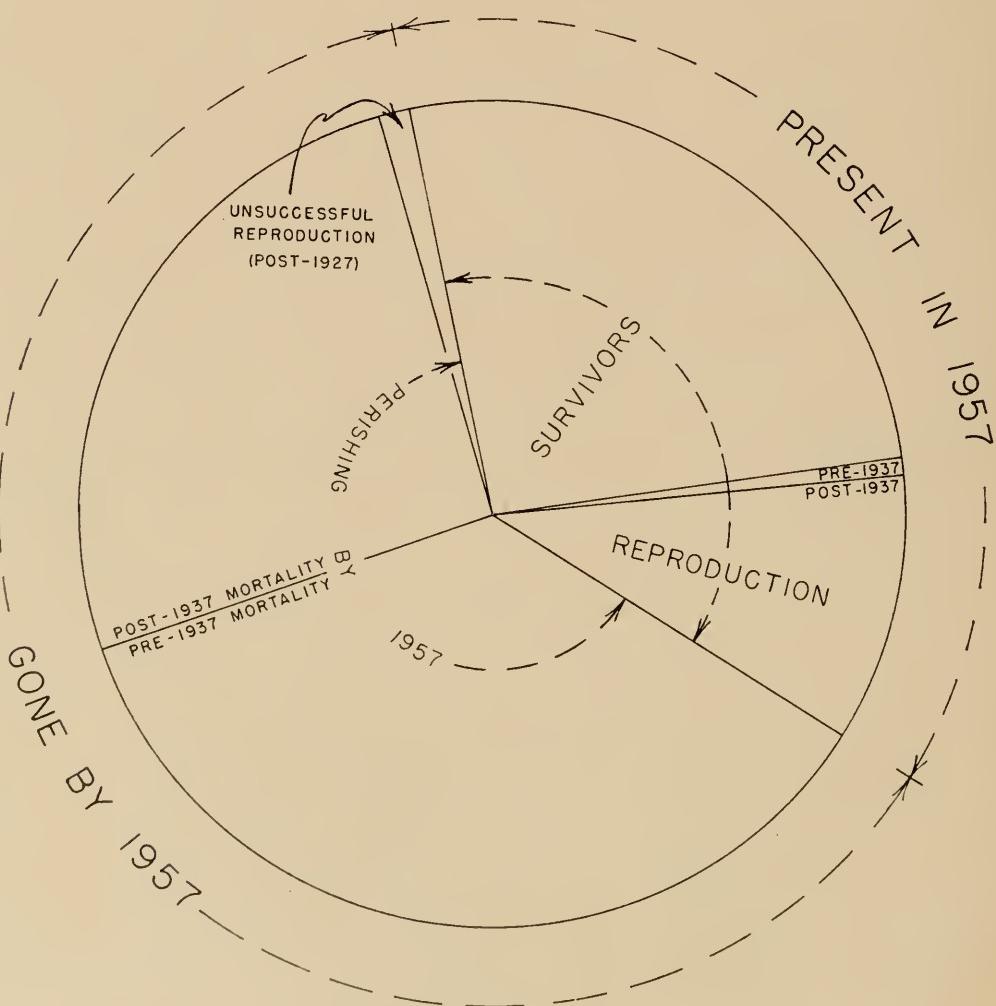


Fig. 9—The appearance, survival, or death of the 4,963 stems on the sample strips during the 30 years.

Among the major species which increased in basal area (Table 6), the three members of the black oak group (red, scarlet, and black) had negligible reproduction in relation to their surviving stems, indicating a failure of reproduction. Their gains in the proportion of the basal area upon the Plot were not accompanied by any increase in numbers.

Black birch, another major species that increased in proportional basal area, recruited 115 stems to the persisting 124. Although red maple declined in proportional area, it recruited 140 stems to the persisting 422. Among the remaining major species on the Plot, white oak failed to reproduce, and the bigtooth aspen gained a single recruit, while the ash added 27 recruits to the 66 persisting stems.

Among the minor species with increases in proportional area, sugar maple recruited at about the same rate as red maple, while tuliptree and shagbark hickory had low reproduction. Of the three remaining minor species which lost proportional basal area, yellow birch was as outstanding as black birch among the major species.

Table 7. The percentage of black birch recruits from 1937 to 1957 according to substrate

<i>Substrate</i>	<i>Percentage</i>
soil bared by man . . . . .	19
chestnut stumps . . . . .	20
near chestnut sprouts . . . . .	2
soil mounds . . . . .	6
rocks . . . . .	6
undetermined . . . . .	47

Among the 12 species classed as unimportant because of their very small contribution to basal area, one-half failed to recruit any new stems. Yet beech, sassafras, and American chestnut recruited many, mostly by sprouting.

About half of the recruits were known sprouts. Actually, this proportion must have been greater, because we recognized as sprouts only those stems with previously measured companion stems, when, in reality, single sprouts may appear on old root systems. If we eliminate black birch, a species reproducing largely by seed, we find that about two of every three recruits of all others were sprouts.

The percentage of known sprouts among trees in 1927 was 39; in 1957, it was 45. Not all species had the same change in proportion of sprouts, however. For example, the percentage of sprouts in red oak increased from 34 to 43 per cent in the 30 years, while in red maple, it changed from 58 to 57 per cent.

Black birch, an exception to the rule of sprouting, invaded specialized seedbeds. Thirty-nine per cent arose on bare soil and stumps (Fig. 10 A), seedbeds indirectly provided by man. Only 12 per cent of the black birches arose on such natural substrates as rocks (Fig. 10 C), and bare soil mounds of windfalls (Fig. 10 D).

Seedling scarcity for other species was not for want of seed, because heavy crops of sound seed appeared in oaks and hickories in 1958, one of the three years when seed crops were examined in detail on the Plot. In subsequent years, however, few nuts were produced; and they were weevily. Many fell prematurely. This established that seed sources were not lacking on the Plot, but that sound and abundant seed was produced only at intervals.

Planting of germinated red oak acorns in late spring was largely unsuccessful because most of the nuts disappeared (Table 8). On scarified soil, less than 1 per cent produced seedlings; but beneath litter, one-fifth succeeded.

Cover, as well as substrate for seed, could affect reproduction. The cover in 1958, however, was not related to reproduction.

Several features of reproduction on the Plot stand out. Oak, which dominates the Plot, is scarcely reproducing. Over 90 per cent of the recruits of all species of trees are contributed by less than one-third of the species. More than half of the recruits were sprouts; the only species recruiting many seedlings, black birch, is doing so on specialized seedbeds;



Fig. 10—A. Black birch (arrows) arising on stumps of an American chestnut. B. The stump beneath this black birch has rotted, leaving the birch propped among fragments of chestnut (arrows). C. Black birch arising on a moss-covered stone. D. Black birch arising on the soil mound of a windfall. The left arrow points at a root at the former height of mound. The right arrow points at the black birch which has slumped and straightened as the mound settled.

the lack of seedlings is not due to lack of seed; and late spring planting of acorns in litter can succeed.

**Defects.** In order to learn whether the future forest would be sound, we examined defects among suppressed stems, which included the recruits, and which were the candidates for the canopy. As expected, the scarlet oak, which is poorly self-pruned (Hepting and Kimmey, 1949), had the highest frequency of defects (Table 9). Even among the other species of oak, more than half the trees were defective. Dead tops and crooked stems were the most frequent defects of oak as well as maple. Trees of diverse species with dead tops were frequently clustered together. In 1957, many standing, dead white oaks, and one with dead tops, were seen.

Table 8. Survival of germinated red oak acorns planted

	Acorns planted May, 1961	Seedlings present September, 1961
scarified soil . . . . .	497	4
litter-covered soil . . . . .	62	12

The birches and tuliptrees had relatively few defects. Although *Necotria* cankers were commonly seen on black birch, stem scars caused by such cankers were not the predominant defect noted for the species. Unimportant in amount (and therefore omitted from Table 9), beech and sassafras, both root-suckering species, had few defects.

Table 9. Defects in suppressed trees on the sample strips

	All individuals	Per cent defective	Tilt	Stem			Crown		
				Bow	Crook	Scar	Break	Top death	Vine
<i>Major species</i>									
red oak . . . . .	41	59	4	2	7	1	3	7	0
scarlet oak . . . . .	6	83	1	1	1	0	1	1	0
black oak . . . . .	18	72	1	1	5	2	1	3	0
black birch . . . . .	211	36	11	5	19	14	9	9	9
red maple . . . . .	450	54	18	23	51	49	49	53	0
white oak . . . . .	68	65	3	4	4	6	2	25	0
white ash . . . . .	64	56	3	1	13	2	4	13	0
<i>Minor species</i>									
sugar maple . . . . .	70	56	0	3	11	1	9	15	0
tuliptree . . . . .	6	33	0	0	0	1	1	0	0
shagbark hickory . . . . .	12	42	1	1	1	0	1	1	0
yellow birch . . . . .	75	39	1	6	7	3	6	4	2
pignut hickory . . . . .	28	54	0	0	4	0	4	7	0

A comparison of the defectiveness of dominant or older with suppressed or younger oaks and maples is shown in Table 10. Unexpectedly, the younger stems were even more defective than the older ones. To conclude the survey of defects, only one-third of the numerous small birch trees were defective; but over half the predominant oaks and numerous maples were defective, and the young ones were no sounder than the old.

*Death.* Mortality, not reproduction, has brought about the significant change in the Plot during the three decades. Consequently, the densities per acre of trees 3 in. d.b.h. and greater fell from 416 in 1927 to only 293 in 1957.

Table 10. Defective oaks and maples

Species	Suppressed Class IV		Dominant Class I	
	Sample size	Per cent defective	Sample size	Per cent defective
red oak . . . . .	41	59	135	59
scarlet oak . . . . .	6	83	58	40
black oak . . . . .	18	72	42	62
white oak . . . . .	68	65	33	55
red maple . . . . .	450	54	7	43
sugar maple . . . . .	70	56	1	0

The density of trees greater than 0.6 and 0.5 in. d.b.h. fell from 1,260 to only 536 in the three decades (Fig. 9).

In almost all species, more of the individuals present in 1927 died than persisted (Table 6, columns 8 and 4). This was even true of three of the four species of the predominant genus, oak, and of the important black birch. Death removed all or almost all black cherry, American elm, bitternut hickory, red cedar, and butternut.

Most deaths were among the small stems. During the three decades, 71 per cent of the stems disappeared, but only 30 per cent of the larger (3 in. d.b.h. and greater) disappeared. Of the 77 still larger trees (10 in. d.b.h. and over in 1937) only 6 per cent died between 1937 and 1957. Finally, in 1957 the modal diameter of the trees that had died in the 30 years was in the smallest size class while it was fully 3 inches for those that persisted.

The high mortality of small plants is also seen in the falling number of shrubs and small trees on the Plot (Table 11). Only one-fifth as many of these six species were found on the Plot in 1957 as were present 30 years before. Flowering dogwood was the only species whose numbers were not drastically reduced; in fact, it increased slightly in the last decade.

The annual mortality rate fell significantly from 51 trees per acre during the first decade and reached 19 during 1938-1957. In the first decade an average of 40 trees disappeared from each thousand present in 1927, and then in the last two decades only 15 trees disappeared from each thousand present in 1937.

After the growing season of 1958, 1959, and 1960, the mortality of the preceding years was found to be 6, 18, and 12 trees per acre, showing the year-to-year variation.

During the same 3 years, the mortality of 10 species of shrubs and trees was recorded. The mortality was least in 1958 in 9 out of 10, and greatest in 1959 in 8 out of 10 of the species, varying from year-to-year in the same cycle as in the trees.

*Frequency.* The net result of the presence of trees on the sample strips in 1927, of reproduction, and of mortality, created the expected distribution of the individuals of each species over the area. In other words, the most numerous species were the most dispersed, with no clustering indicated.

Table 11. Reduction in number of stems of certain shrubs and small trees

Species	No. of stems to the acre		
	1927	1937	1957
blue beech . . . . .	290	181	62
gray birch . . . . .	151	58	2
hop hornbeam . . . . .	50	30	22
flowering dogwood . . . . .	17	13	14
shadbush . . . . .	39	31	4
witch hazel . . . . .	77	24	20
Totals	624	337	124

## DISCUSSION

The climate and past land use, as well as the dominance of oak and the lack of other communities, identified the Plot as a typical oak forest of the Central Hardwood Region. This, and the age of the stand, make it typical of many thousands of acres of Connecticut woodland. The soil or site, however, may make it better than many.

The 70-foot height of 60-year-old trees on the wet, as well as dry, sites of the Plot shows the growth to be better than three of six sites indexed in the Central and Northern Hardwood Regions of Pennsylvania (McIntyre, 1933). The basal area on the Plot, 75 square feet per acre in 1927 and 117 in 1957, was also better than on three of six site classes in Pennsylvania.

On the Plot in 1927 and 1957 the densities of trees 3 in. d.b.h. and greater were 416 and 293, almost identical to the 439 and 261 trees per acre in 30-and 60-year-old stands on the best sites in Pennsylvania. The mean d.b.h. on the Plot in 1927 was 5.7 inches, typical of a 30-year-old stand on a good site (index 70) in Pennsylvania. All these data illustrate the consistency of growth and form of trees throughout the Region.

The high quality of the Plot is not surprising, for the slopes are gentle, rock outcrops are uncommon, and the deep soil has a fine sandy loam texture that enhances storage of water.

The decrease in the density of trees reflects the low reproduction rate. Low as it may be, it has certainly increased in the recent decades. Why did the number of recruits increase eightfold from the 1927-37 period to the 1937-57 period? We might explain this very readily if mortality rates had increased and created more vacancies in the canopy for new stems to fill. However, mortality declined, so we cannot use such an explanation.

We have attributed the decline of shrub thickets and small stems, and the general absence of reproduction by seedlings, to a lack of light. If a temporary spurt of growth of small stems occurred, many would reach measurable size. Such growth would be caused by a change in forest structure that admitted more light. It would not be necessary for dominant trees to be toppled to gain additional light; more light could be admitted if trees were tilted, or if widespread breakage of branches occurred. In fact we saw that; the trees were tilted. Because the outstanding storm since 1927 was the 1938 New England hurricane, which came ashore east of the Plot and felled trees westward in less sheltered forests, this tilting is not surprising. The numerous broken tops are tabulated in Table 9. Thus, we believe that the tilting of the trees in 1938 together with occasional ice storms caused the increase in recruiting between 1937 and 1957. We cannot predict when it will happen again.

The failure of oak to reproduce could be attributed to the failure of existing stems to grow in the shade of other oaks. The failure of a species to grow under its own kind has been noted by others (Britton, 1906) and is doubtless one of the mechanisms by which succession is accomplished. The lack of openings in the canopy, the decline of once vigorous shrub thickets, and the observed slow height growth of existing small stems all suggest that light conditions are not favorable at the shrub level. Even if light were adequate, a failure could also be caused by lack of seed. But the periodic production of sound seed has been observed on the Plot.

Undoubtedly, however, the overwinter removal of seed by rodents prevents the success of the seed. In particular, white oak acorns produced on the Plot were the first to disappear. Even when germinated red oak acorns were set out in the spring, most were removed. If the spring-planted acorns were hidden beneath litter, however, a considerable number did survive, while less than 1 per cent survived on scarified sites. We shall see, though, that the apparently detrimental scarification process is beneficial to the most successful recruiter of seedlings, the light-seeded black birch.

The gains in the number of black birch can be largely credited to man. It is essential for birch to begin on a litter-free seedbed as shown by Table 7. This requirement is fulfilled by low chestnut stumps (Fig. 10A) with a rotting core of organic matter. Birches arising from chestnut stumps can often be recognized years later by their propped root system when only fragments of the stump remain (Fig. 10B). Although stumps of other species existed in the forest from time to time, they did not persist or form a rotten core with a resistant shell of wood as did chestnut. Unless man had cut off chestnut stems, this specialized seedbed would not be available, for after the blight the uncut chestnut stems eventually toppled over (Fig. 3), leaving no stump to form a raised, litter-free seedbed. The increasing

diameter of growing birches inside these natural "planting pots" breaks them apart. Thus, now that chestnut is blighted and no longer reaches a large size, this specialized seedbed will disappear. The other important seedbed was the litter-free ruts of old woodroads. Again, this was created by man.

The naturally created seedbeds are soil mounds and rocks with moss or cracks. Had wind uprooted more trees and created more mounds, more birch would likely have grown on them. Elsewhere in Connecticut where forests have been subjected to greater windthrow and soil mounds are common, black birch is a more important species, in some places dominating the more exposed eastern slopes. The future of birch in the Plot cannot be foretold.

Red maple increased mostly by sprouting. While it may sprout almost endlessly on the same root system, it seems to be merely marking time. If such sprouts reach a large size before dying, they may decay and provide an avenue for rot to enter the main stem in the clump. The tendency of sprout stems to lean outward makes them a larger target that is more vulnerable to loading by ice and snow and to falling stems and limbs than the target offered by a single straight stem. Thus, the increase of red maple stems on Cox Plot is hardly favorable, and as mortality studies showed, many perished.

White ash is prolific and sends up many sprouts. It has lost importance, however, as its decline in absolute basal area shows. The gains in numbers by minor species may appear important relative to their total number of stable surviving stems, but none of these species is sufficiently numerous, or occupies sufficient area relative to all other species, to gain great influence in the immediate future.

Among the 12 unimportant species, the only numerous recruits were sprouts of beech, American chestnut, and sassafras. Although beech can endure shade, it cannot spread far vegetatively. American chestnut is regularly removed by blight. Sassafras cannot endure shade. Apparently, none of these three species will be very important in the coming century if events continue as they have.

Forests of the Northeast commonly reproduce by sprouting. Connecticut is part of the "sprout hardwood region" of Hawley and Hawes (1912) and the greater part of its forests are said to have originated from sprouts (Frothingham, 1912). Oak forests of Pennsylvania (McIntyre, 1936) are estimated to be 75 per cent of sprout group origin. It has been shown that many of the "seedlings" of oak forests in southeastern Ohio are as much as 31 years old (Merz and Boyce, 1956). Certainly, on the Cox Plot sprouts are prevalent.

Their prevalence is readily explained. Repeated cutting of genera capable of sprouting, such as oak and maple, has permitted their rapidly growing sprouts to outstrip slower growing seedlings. Before blight removed chestnut, its prolific sprouting after cutting had permitted it to dominate the earlier forest (Korstian and Stickel, 1927).

The sprout habit determines whether a stem resembles a tree or a shrub. Sprouts may arise from the dormant buds of a root collar (stump sprout), from adventitious buds in callus (stool sprouts), and from adventitious buds in roots (root suckers) (Hawley and Smith, 1954). The point of origin for the sprout is critical and the height above ground where a

sprout arises determines its survival, strength, and resistance to decay (Roth and Hepting, 1943). Any factor which kills part or all of the above-ground portion of a woody plant while leaving the root system unharmed may initiate sprouting. Among factors which do this are fire, drought, top breakage, death in the top from insect defoliation, cutting by man, and girdling or browsing by mammals.

Sprouting can be beneficial. It overcomes or minimizes such hazards of seedling reproduction as destruction of seed, drying of surface soil, root competition, heat injury, and damping off. Furthermore, the growth on an already established root system is greater than seedling growth, which can proceed no faster than its root system can develop. Such rapid growth reduces the time that the growing tip is exposed to browsing mammals and shading. The many spreading stems in the sprout clump shade seedlings and give the sprout an advantage because their foliage covers a larger area than might be covered by a single-stemmed tree. The rapid growth often results in knot-free sawlogs.

These advantages are sufficiently great for red oak that the proportion of sprouts had increased upon the Plot from 34 in 1927 to 43 in 1957. This is the consequence of the fully 42 per cent sprouts among the few recruits and only 27 per cent sprouts among the many dying.

Disadvantages, however, also accompany sprouting. These appear as the sprout grows older or is shaded. The crowding of stems on a stump causes some to lean outward. Such stems are competing with each other for light, and no one stem can make the maximum use of materials entering the clump. Although the death of companion sprouts in a clump may enable one to survive and "straighten up," a curve at the base of the tree (termed "sweep" by foresters) persists and reduces the value of the log because of loss in sawing.

The leaning stems accumulate great loads of ice and snow which may break them from the clump. Their asymmetry makes them more easily toppled by winds. The target area of the clump increases its chance of being hit when nearby stems or branches fall (Fig. 11). If the companion sprouts in a clump are overtapped and die, the upper limbs in the surviving stem may enlarge into the vacated space. Then if these limbs are later shaded and die, they provide a larger wound than that provided by the death of a small limb. The wounds from these processes admit fungi and insects which weaken the stem and contribute further breakage (Hepting *et al.*, 1940; Toole, 1961).

All these faults in the case of the overtapped red maple must have handicapped it. Unlike oak, its proportion of sprouts changed very little. From 1927 to 1957 sprouts declined from 58 to only 57 per cent. The proportion of sprouts within the group that died and which appeared was respectively 59 and 58 per cent.

The faults of sprouting can also be seen in the black birch. Because only 10 per cent of the recruits were sprouts and fully 50 per cent of the dying were sprouts, the proportion of sprouts in the black birch population fell from 55 to 27 per cent during the three decades. The deficiencies of birch sprouts are revealed in the better survival of the population with the lower proportions of sprouts: the population that survived the three decades had only 45 per cent sprout stems whereas the population that disappeared after 1927 was composed of 57 per cent sprouts.

And finally, sprouting preserves the composition of the stands and whatever virtues or faults may be inherent in that composition. For instance, the tops of some trees and shrubs may never exceed a century or two in age, but their root systems and genotypes could be thousands of years old (Curtis, 1959). The genotype, be it suitable or not, is maintained by this type of reproduction. Furthermore, rapidly growing sprouts overwhelm the slower growing seedlings, reducing variability and opportunity for natural selection. Sprouting may permit an individual to survive in an environment rendered unsuitable by succession or climatic change. It favors the longevity of roots and likely favors root grafts. These provide routes for pathogens.

A genetically homogeneous population undergoing no turnover may lack capacity to adapt to changing conditions of its environment, whether those changes are purely physical changes of the stand climate or increased virulence of a plant disease. Sprouting then, restricts genetic variability and conserves traits of the sprout parent. Only sexual reproduction provides the variability and opportunity for natural selection among new seedlings and genotypes which are produced. Thus, evolution of the plant community which could bring it into better equilibrium with the site is slowed or prevented by sprout reproduction.



Fig. 11—When the dead stem (right) fell and struck the blue beech clump, a leaning sprout was broken from the clump.

The greater extent of defect in small or young stems, compared to large or old stems (Table 10), offers little hope that recruits will automatically improve the forest. If anything, the small stems will acquire more defects as time passes and subjects them to hazards. A natural release of present small stems would compound the defects of the forest. There is nothing in the data to suggest an automatic correction of defects. If general improvement takes place in the stand, it will probably do so on a geological time scale rather than over a human life span.

Mortality, not reproduction, is the overwhelming influence on the Plot (Fig. 9). Climate undoubtedly contributes greatly to its year-to-year variation, for the high mortality of 1959 followed the cold, dry gale of January 4-6 when snow cover was lacking. Another environmental factor, soil moisture deficiency, would explain the clusters of dead tops of different species. The decline of mortality over the decades, however, is merely the usual habit of maturing forests.

The forester uses death to improve the forest according to his wishes. He kills the larger undesirable tree and permits the desirable small trees beneath to grow. If large trees were dying in the Plot, a revolution would be brewing. However, it is the small trees that are dying. Therefore, the undisturbed woodland is becoming more homogeneous, not more diverse.

The black oak group is increasing in dominance (Table 6); the forest is becoming more susceptible to the present problems characteristic of oak woodlands; and the approaching monoculture is conceivably as subject to catastrophe as was the chestnut. This prediction of stability is, of course, applicable to decades and not centuries. Sudden intervention by man or a violent windstorm or disease could change all this. Nevertheless, since death, not birth, is the controlling process, the composition of the Plot was established for a third of a century by its composition in 1927. It is probable that this composition will continue for decades to come.

## CONCLUSIONS

1. The trees on Cox Plot, an unmanaged oak woodland that has developed on land abandoned or cutover 75 years ago, have grown tall, for the site is good. Nevertheless, the forest has undergone surprisingly little change in appearance or composition in the past three decades.

2. What changes have occurred have been shifts in importance caused by growth and mortality. These shifts have included the disappearance of certain pioneer species such as red cedar, aspen, and black cherry that are common to old fields, and the increased growth in basal area of oak. The natural trend is away from the original diversity of species and towards a stand increasingly dominated by oak.

3. Reproduction has had a negligible influence in changing the forest, primarily because the area is saturated with competing stems, leaving little opportunity for new ones. This is confirmed by the greater mortality of small than of large stems and by the poor development of plant layers beneath the canopy. Furthermore, the reproduction that has occurred has been largely vegetative. It has failed to extend the influence of the new sprout stems very far and, in fact, will probably handicap the stems to which they are attached.

4. The nearly continuous canopy with its shade is probably the structural feature that most inhibits reproduction by seedlings. However, the sparseness of the understory is maintained by browsing animals and the periodic crops of seed are mostly destroyed by eaters of seed. Today the location of the Plot protects it from wind, but when the defect in the present stems increases, trees of the Plot may be broken, light admitted to lower layers, and the vegetation once again may become diverse.

5. Should the canopy open, as it might following wind and ice storms, the replacement stems will probably compound the amount of defect already present because the suppressed stems are still more defective than the dominant ones. This in turn should hasten population turnover.

6. Without populatioin turnover and variability introduced by seedling reproduction, there can be no natural selection of types best suited to the site.

7. The changes in forest composition were slight when judged by the standard of a human lifespan. As the once prevalent, small-scale, diversified agricultural and cutting practices have diminished, so too have the periodic disturbances and abandonments of land diminished. These were the causes of the diverse landscape mosaic of the past.

8. To the extent that the Plot mirrors the history of countless other woodlands in southern New England, it explains the trend away from diversity toward a woodland increasingly dominated by oaks. Since intervention by man, windstorm, or pest seems necessary to change this course, decreasing diversity will probably be the rule for years to come.

## SUMMARY OF OBSERVATIONS

The three decades of change in permanent plots in an unmanaged woodland in Central Connecticut can be summarized in a dichotomous key to changes in numbers and basal area of the species:

	<i>Relative basal area in 1957</i>
A. Species eliminated from sample strips in 30 years	red cedar butternut 0%
AA. Species present in sample strips	
B. Species increasing in number of stems since 1927 or 1937.	black birch chestnut oak beech American chestnut 9%
BB. Species decreasing in numbers	
C. Species declining in absolute basal area since 1927 or 1937	white ash bigtooth aspen black cherry American elm 3%
CC. Species increasing in absolute basal area	
D. Species initially increasing in absolute area, but later reduced, not necessarily to original absolute volume	white oak pignut hickory 13%
DD. Species maintaining a steady increase in absolute basal area	
E. Species declining in relative basal area, but maintaining an increase in absolute basal area	red maple yellow birch mockernut hickory bitternut hickory tupelo 16%
EE. Species increasing in both relative and absolute area	
F. Minor and unimportant species, none ever contributing 5 per cent of relative basal area	sugar maple tuliptree shagbark hickory basswood hemlock 7%
FF. Major species, each contributing 5 per cent or more relative basal area at any time during the study	red oak scarlet oak black oak 51%

**COMMON AND SCIENTIFIC\* NAMES OF PLANTS  
MENTIONED IN THIS BULLETIN**

Ash, white— <i>Fraxinus americana</i>	Hazelnut— <i>Corylus</i> sp.
Aspen, bigtooth— <i>Populus grandidentata</i>	Hemlock— <i>Tsuga canadensis</i>
Azalea— <i>Rhododendron</i> sp.	Hickory, bitternut— <i>Carya cordiformis</i>
Basswood— <i>Tilia americana</i>	shagbark— <i>Carya ovata</i>
Beech— <i>Fagus grandifolia</i>	mockernut— <i>Carya tomentosa</i>
Birch, black— <i>Betula lenta</i>	pignut— <i>Carya glabra</i>
yellow— <i>Betula lutea</i>	Hop hornbeam— <i>Ostrya virginiana</i>
gray— <i>Betula populifolia</i>	Juniper, common— <i>Juniperus communis</i>
Blue beech— <i>Carpinus caroliniana</i>	Maple, sugar— <i>Acer saccharum</i>
Blueberry, highbush— <i>Vaccinium corymbosum</i>	red— <i>Acer rubrum</i>
Butternut— <i>Juglans cinerea</i>	Oak, white— <i>Quercus alba</i>
Canada mayflower— <i>Maianthemum canadense</i>	chestnut— <i>Quercus prinus</i>
Catbrier— <i>Smilax</i> sp.	red— <i>Quercus rubra</i>
Cedar, red— <i>Juniperus virginiana</i>	scarlet— <i>Quercus coccinea</i>
Cherry, black— <i>Prunus serotina</i>	black— <i>Quercus velutina</i>
Chestnut, American— <i>Castanea dentata</i>	Pine, white— <i>Pinus Strobus</i>
Club moss— <i>Lycopodium</i> sp.	Sassafras— <i>Sassafras albidum</i>
Dogwood, flowering— <i>Cornus florida</i>	Shadbush— <i>Amelanchier arborea</i>
Elm, American— <i>Ulmus americana</i>	Spicebush— <i>Benzoin aestivale</i>
Fern, ebony spleenwort— <i>Asplenium platyneuron</i>	Sumach, poison— <i>Rhus vernix</i>
Christmas— <i>Polystichum acrostichoides</i>	Sweet pepperbush— <i>Clethra alnifolia</i>
New York— <i>Dryopteris noveboracensis</i>	Tuliptree— <i>Liriodendron Tulipifera</i>
Grape, wild— <i>Vitis</i> sp.	Tupelo— <i>Nyssa sylvatica</i>
	Witch hazel— <i>Hamamelis virginiana</i>

\* Scientific names follow Fernald, 1950.

### Literature Cited

- BARD, G. E., 1952. Secondary succession on the Piedmont of New Jersey. *Ecol. Monographs* 22:195-215.
- BRITTON, N. L., 1906. The hemlock grove on the banks of the Bronx River and what it signifies. *Trans. Bronx Soc. Arts Sci.* 1:5-13.
- BUELL, M. F. AND J. E. CANTLON, 1953. Prescribed burning effects on ground cover in the New Jersey pine region. *Ecology* 34:520-528.
- COLLINS, S., 1957. The biotic communities of Greenbrook Sanctuary. *Palisades Nature Association*, Englewood, N. J.
- CURTIS, J. T., 1959. The vegetation of Wisconsin. *Univ. of Wisc. Press*, Madison, Wisc.
- FERNALD, M. L., 1950. Gray's manual of botany, 8th ed. Amer. Book Co., New York.
- FROTHINGHAM, E. H., 1912. Second growth hardwoods in Connecticut. *U. S. Forest Serv. Bull.* 96.
- HAWLEY, R. C. AND A. F. HAWES, 1912. Forestry in New England. John Wiley & Sons, Inc., New York.
- HAWLEY, R. C. AND D. M. SMITH, 1954. The practice of silviculture. 6th ed. John Wiley & Sons, Inc., New York.
- HEPTING, G. H. *et al.*, 1940. External features correlated with top rot in Appalachian oaks. *J. Forestry* 38:873-876.
- HEPTING, G. H., AND J. W. KIMMEY, 1949. Heart rot. *U. S. D. A. Yearbook*.
- HICOCK, H. W. *et al.*, 1931. The relation of forest composition and rate of growth to certain soil characters. *Bull. 330, The Conn. Agr. Exp. Sta.*, New Haven, Conn.
- KORSTIAN, C. F. AND P. W. STICKEL, 1927. The natural replacement of blight-killed chestnut in the hardwood forests of the northeast. *J. of Agr. Res.* 34:631-648.
- LUTZ, H. J., 1928. Trends and silvicultural significance of upland forest successions in southern New England. *Yale Univ. School Forestry Bull.* 22.
- MCINTRYE, A. C., 1933. Growth and yield in oak forests of Pennsylvania. *Bull. 283, Penn. State Coll., School Agr. and Exp. Sta.*
- \_\_\_\_\_, 1936. Sprout groups and their relation to the oak forests of Pennsylvania. *J. Forestry* 34:1054-1058.
- MERZ, R. W. AND S. G. BOYCE, 1956. Age of oak "seedlings." *J. Forestry* 54:774-775.
- RAUP, H. M., 1940. Old field forests of southeastern New England. *J. Arnold Arboretum* 21:266-273.
- ROTH, E. R. AND G. H. HEPTING, 1943. Wounds and decay caused by removing large companion sprouts of oak. *J. Forestry* 41:190-195.
- TOOLE, E. R., 1961. Rot entrance through dead branches of southern hardwoods. *Forest Sci.* 7:218-226.
- TRIMBLE, G. R., JR. AND S. WEITZMAN, 1956. Site index studies of upland oaks in the northern Appalachians. *Forest Sci.* 1:162-173.



